

Changes Induced by Elk Herbivory in the Aboveground Biomass Production and Distribution of Willow (*Salix monticola* Bebb): Their Relationship with Plant Water, Carbon, and Nitrogen Dynamics

By

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Abstract. Willows are dominant woody plants of many high-elevation riparian areas of the western USA, and constitute an important food resource for various ungulates, which tend to concentrate in riparian areas. The response of willow to grazing was analyzed in the elk winter range of Rocky Mountain National Park, by considering the effect of elk grazing on *Salix monticola* Bebb, one of the most common willow species in this area. Ungrazed and grazed treatments were established during the 1997 growing season (May to October), using eight long-term exclosures built in the fall of 1994. Plants in the grazed treatment were in areas open to grazing, but were protected from grazing by small exclosures during the experimental period. Winter grazing by elk induced the following measured responses in plant morphology and development: (1) higher shoot biomass production but similar leaf biomass and leaf area per plant, (2) a lower number of and bigger shoots, (3) a lower number of and bigger leaves, and (4) flower inhibition. In addition, we infer that grazing induces lower belowground allocation and a more negative nitrogen (N) balance but a higher soil N uptake. We conclude that elk grazing negatively affects willow even though willow compensate for aboveground biomass removal. Continuous grazing produces long-term changes in willow morphology that constrain plant growth and development. High plant utilization, as occurred in this experiment, could therefore reduce the competitive ability and survivorship of willow, in particular under drier environmental conditions.

Keywords: *Cervus elaphus*, grazing, plant-animal interactions, riparian ecosystem, Rocky Mountain National Park, *Salix monticola*.

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Introduction

Ungulate activities modify ecosystem structure and function (Naiman 1988). Large herbivores directly affect plants through tissue removal, but they can also induce long-term changes in nutrient cycling (Detling 1988; Huntly 1991; Pastor and Naiman 1992; Hobbs 1996), which can modify the competitive ability of a particular plant species or functional group (Bryant 1987; Pastor and Naiman 1992). At the plant level, removal of plant tissues by ungulates causes morphological and physiological changes in the plant over a broad range of temporal scales (Briske and Richards 1995). However, most of the information regarding plant responses to herbivory is based on studies conducted on grasses, and the literature on the response of woody plants to defoliation is limited. Several differences are expected between graminoid and woody plant responses, due to plant characteristics and different patterns of ungulate tissue removal. Woody plants have a juvenile and mature stage of development, with an age trend in aboveground annual woody biomass production. Tissue removal can induce changes in this development pattern (du Toit et al. 1990) determining long-term morphological changes (Bergström and Danell 1987). Strategies to prevent grazing differ from those of herbaceous plants (Rohner and Ward 1997), and involve physical responses such as the production of thorns (Gowda 1996; Cooper and Ginnett 1998), chemical defenses (Bergström 1992; Herms and Mattson 1992), and unique growth strategies (Bergström 1992). Many woody plants are grazed during the period of dormancy, with a lag phase between the occurrence of grazing and manifestation of a plant response (Danell et al. 1994). Finally, foraging selectivity of browsers of woody plants is higher than that of grazers of herbs (Hofman 1989; Bergström 1992), and plant responses depend on the type and time of tissue removal (du Toit et al. 1990; Bergström 1992). These characteristics can result in important differences between woody and graminoid plant responses to defoliation.

In this paper, we analyzed grazing-induced changes in various physiological and morphological characteristics of a riparian willow (*Salix monticola* Bebb). Willows are the dominant woody plants in the high-elevation riparian areas of the western United States (Patten 1998). Large ungulate herds regularly congregate in riparian areas and browse on willows. Thus, these willows have successfully evolved under grazing, and constitute a good model to evaluate woody plant responses to grazing. Additionally, grazing pressure on

willows has increased in recent years in many montane riparian areas due to human interventions (Kay 1994; Patten 1998). These include livestock grazing, but also increases in the concentrations of wild ungulates in riparian areas. Many riparian areas are showing decreases or degradation of willow communities (Patten 1998). Prediction of the effect of ungulate pressure on riparian ecosystem processes is largely dependent on understanding the response of willow to tissue removal. Few studies have been conducted to analyze changes induced by grazing on these riparian willows. In particular, it is not clear how willow physiological processes altered by grazing are linked to plant productivity and survivorship (Singer et al. 1998; Alstad et al. 1999). Higher water potential and higher leaf carbon isotope discrimination was found in grazed *S. monticola* willows than in ungrazed controls, which can improve willow regeneration and survivorship (Alstad et al. 1999). We hypothesized that grazing on willow produces long-term effects in plant morphology determining changes in physiological processes and survivorship. Our study had the following primary objectives: (1) to determine aboveground biomass production and distribution in willows under grazing and non-grazing conditions; (2) to relate biomass production and morphological changes induced by grazing to plant performance; and (3) to infer how elk (*Cervus elaphus*) grazing affects plant survivorship.

Materials and Methods

The experiment was carried out during the 1997 growing season (May to October), on willows growing inside elk exclosures, and on paired plots adjacent to each exclosure and open to grazing. Four exclosures (30 x 46 m) were built in August and November 1994 in short willow (<1.5 m height) communities, at each of the following sites in Rocky Mountain National Park (RMNP), Colorado: the Moraine Park area in the Big Thompson River watershed (2,481 m altitude) and the Horseshoe Park area in the Fall River watershed (2,598 m altitude). Two treatments were established: the ungrazed treatment consisted of two plants inside each exclosure, and the grazed treatment comprised two plants of a paired plot open to grazing until May 1997. At this time, small exclosures were built around each selected plant to prevent removal of new tissues formed during the course of the experiment. To select plants, we identified in each plot (exclosure or paired grazed area) all *S. monticola* that represented the most frequent size

type (canopy volume and height) within the plot. From this subset we randomly chose two plants per plot. *S. monticola* is one of the dominant willow species in these watersheds, and is a common willow in the lower-elevation riparian areas of the northern Colorado Rocky Mountains (Cottrell 1995). Mean winter consumption of willow by elk was estimated to be as much as 28% in both study valleys and for the entire willow cover (Singer et al., this volume). However, the utilization of short willow tends to be higher, though not significantly so, because elk tend to concentrate in the area of short-willow communities and in open meadows. During the winter, elk concentrate at densities as high as 66–110 elk km⁻² in Moraine Park, and at lower densities in Horseshoe Park (15 to 30 elk km⁻²; Singer et al., this volume). No other ungulates concentrate in such dense herds in these valleys, so willow grazing is almost entirely due to elk.

Soil moisture was monitored on a weekly basis in all plots with a time domain refractometer, Trace System model 6050 1. Due to soil depths, measurements were made between 0 and 28 cm in Moraine Park and 0 and 58 cm in Horseshoe Park. Measurements were taken under the canopy of the selected plants and in the adjacent area between willow canopies. Groundwater depths were monitored each month on wells installed inside the exclosures and in the grazed areas (Zeigenfuss et al., this volume). During the growing season, we determined the time periods of the phenological phases for a representative sample of stems of different sizes (six to eight target stems) in each of the selected plants. Plants were visited every 2 weeks from 10 May until the end of October. Bud break, flowering, seed dispersal, and leaf shedding were determined by visual observation of the target stems. The phenological phase was considered initiated when more than 50% of the marked stems were in this phase. The number of 1997 shoots in the target stem was counted approximately every 2 weeks, and one shoot at the top of the stem was selected for measurements of shoot length, leaf number, and the length of the longest leaf. On each sample date, several ungrazed 1997 shoots from adjacent *S. monticola* plants were collected to determine the morphological variables described above, and the total leaf area of each shoot. These data were used to create a multiple linear-regression model of leaf area per shoot using shoot morphological variables as predictors. For each shoot and date, morphological variables were transformed to leaf area and multiplied by the total number of 1997 shoots on the stem. Leaf area per stem was expressed as a ratio to the maximum leaf area value of all measurement dates within the stem.

Gas exchange measurements were performed on selected plants during the second week of June on leaves of the upper canopy of the 32 selected plants. A second set of gas exchange measurements was made on fully developed leaves in the upper portion of the canopy on the second week of July. Leaves were repeatedly measured throughout the day, on 2 days, on two plants growing in the same exclosure and two plants in the associated grazing plot. Between July 17–22, a third set of measurements was made on five plants per treatment on leaves located at different positions in the canopy. All gas measurements were made with a LI-COR LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska) equipped with a 0.25-l leaf chamber. We discarded gas exchange data from any run in which the standard error of the slope of the CO₂ concentration over time was greater than 10% of the value of the slope (LI-COR 1990). We also discarded data with an error higher than 20% between the estimation of transpiration using the relative-humidity method and the estimate using leaf energy balance (LI-COR 1992).

During the first week of September before leaf shedding started, we harvested eight plants per treatment (one per exclosure and paired plot) by cutting all stems at ground level. We measured the total dry weight of woody and leaf biomass of each stem of the harvested plants. In addition, leaf number and area were measured on all marked stems. A regression model of leaf area on leaf dry weight was constructed for each treatment with measurements performed on the target stems. These regression models were used to estimate total leaf area of the harvested plants. For each stem, shoots (segments of the stem produced each year) of different ages were separated. The age of each stem shoot was identified based on the position of the shoot according to the sympodial ramification pattern of willows, or the scar marks of the stems in the case of older shoots (Alliende and Harper 1989). Ring counts were also performed on some shoots to check the accuracy of the method. In all cases, the predicted age of the two methods gave the same result. Cohorts of shoots were formed by grouping all shoots of the same age within each harvested plant, and total dry weight determined for each shoot cohort.

Nitrogen dynamics were inferred from samples of leaves and 1996 and 1997 shoots taken from: (1) all of the selected plants at four times during the growing season, (2) the 16 plants harvested in the first week of September, (3) the 16 unharvested plants in October, and (4) leaves collected from the soil surface litter in litter traps in October 1997. Nitrogen was also determined in

shoot cohorts from one of the largest target stems of each of the 16 harvested plants. Analyses were conducted with a LECO CHN analyzer and expressed as percent N. In addition, total N of different plant parts was calculated based on biomass and percent N measurements from the harvested plants. Total N in the aboveground woody biomass (PN) of each plant (m) was calculated as:

$$PN_m = \sum_n NS_{n,m} \times SB_{n,m} \quad (1)$$

where NS and SB are the proportion of N and biomass, respectively, of each shoot cohort (n) within a plant. Total N in leaves and shoot cohorts of the harvested plants was calculated in a similar manner. Total N retranslocated back to the plant from the leaves during senescence (RN) and total N lost through litterfall (LiN) were estimated using the following equations:

$$RN_m = (NL1_m - NL2) \times LB_m \quad (2)$$

$$LiN_m = NL2 \times LB_m \quad (3)$$

where NL1 and NL2 represent the proportion of N in leaves prior to and after litterfall (September and October samples, respectively), and LB is the leaf biomass of each of the 16 harvested plants. Note that NL2 is not plant specific.

Statistical Analysis

A complete randomized-block design ANOVA for comparison of experiments was used to analyze most of the measured variables. The enclosure and paired grazed plot were considered as a block, and the ANOVA test was used to check for differences between sites (Moraine and Horseshoe Parks), treatments, or interactions. Treatments were also compared with a covariance (ANCOVA) analysis in the case of biomass variables to account for the effect of initial heterogeneity in plant size. ANCOVA was also used to analyze the relationship between different plant biomass compartments (leaves, 1996 and 1997 shoots). Gas exchange variables of the second set of measurements were analyzed using a nested mixed model, and in the case of the third set of measurements using a t -test of the difference between values taken in the upper and lower canopies. In the latter case, data of both treatments were pooled because of the small sample size. Finally, percent N of different shoot cohorts was compared considering the differences among all combinations of cohorts taken by pairs within

the plant, because percent N values of different cohorts were not statistically independent.

Results

Hydrological Conditions for Willow Growth

Water tables followed a negative trend during the growing season but records were not deeper than 0.5 m during June and July, and not deeper than 1 m during the entire growing season. The volumetric soil moisture followed the same negative trend, except that it was more affected by a rain event that occurred at the end of July 1997. No differences were found in soil water content either between parks, or between versus under willow canopies. Soils were saturated at the beginning of the season and soil water decreased to 39% in the first 0–28 cm at the end July, when it rose to about 46% due to a rain event. Soil moisture steadily decreased in August but values were not lower than 37%. Thus, plants were not water limited during the entire growing season. The observed soil volumetric moisture values corresponded to high soil water potentials, as these are relatively coarse soils (Menezes 1999).

Phenology and Leaf Area Dynamics

The growth period lasted approximately 3 months, from June through August (Fig. 1). Leaves started to develop 2 weeks later in *S. monticola* than in *S. planifolia*, the co-dominant willow species in the study area. Additionally, ungrazed plants started growth a few days earlier than grazed plants. Catkins began to form from buds of previous-year shoots just prior to bud break, and seed dispersal occurred early in the growing season. No catkins were found on the grazed plants. This was not only the case for the selected plants but for all the short willow plants that we checked at different locations in both valleys. Most shoots were differentiated early in the growing season (Fig. 2a). Leaves were formed during the season at the same time as shoot growth, since all leaves developed on new shoots (Fig. 2b,c). In August, changes in the measured variables were minor, indicating that vegetative growth ended during this month. Grazed plants produced fewer shoots per stem than the ungrazed plants (Fig. 2a) but were significantly longer ($P < 0.01$; Fig. 2b). In addition, grazed plants produced fewer leaves than ungrazed plants (411 and 228 mean number of leaves/stem, $P = 0.035$), but leaves were bigger (3.7 and 5.1 cm² leaf⁻¹, $P = 0.015$).

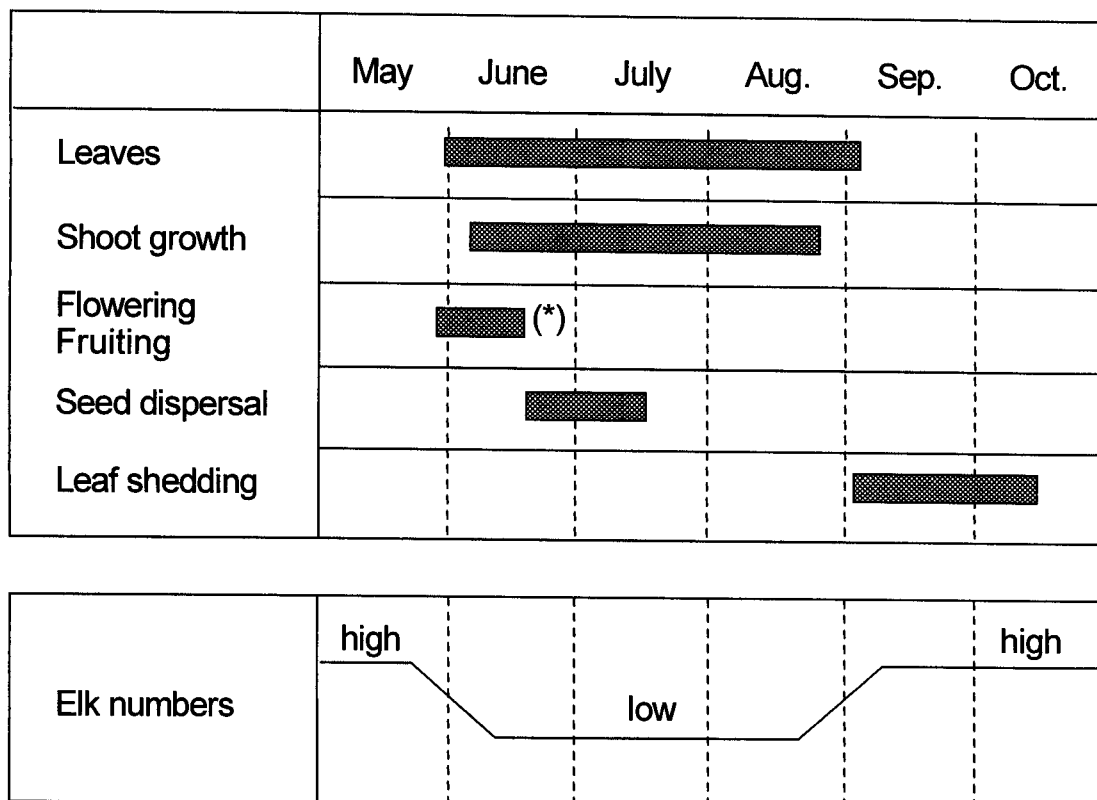


Fig. 1. Phenological phases of *Salix monticola* and relative number of elk on the study areas. (*) no flowers were found in grazed plants.

No differences between treatments were found in specific leaf area [77.1 and 74.2 cm² g⁻¹ ($P = 0.83$) for ungrazed and grazed treatments, respectively]. Total plant leaf area steadily increased during the growing season in a similar manner in both treatments (Fig. 2d). Differences between treatments were significant only on the first date of measurement, probably because the ungrazed plants started growing earlier than grazed plants.

Plant Biomass

Similar ranges of total woody biomass were found in plants of the ungrazed (470–2,720 g) and grazed (380–3,110 g) treatments. Nevertheless, at the beginning of the experiment, plants in the ungrazed treatments were taller (1.71 m vs. 0.92 m; $P = 0.001$) and larger (3.19 m³ vs. 1.36 m³; $P = 0.03$). Ungrazed plants were also taller

at the end of the experiment (1.97 vs. 1.20 m; $P = 0.0003$). Aside from initial differences in plant morphology, total dry weights of woody biomass, leaves, and 1997 shoots were not different at the end of the experiment (Fig. 3). Total plant leaf area was not different between treatments ($P = 0.4$). The range of variation was 1.7–9.4 m² for the ungrazed, and 1.3–6.9 m² for the grazed treatment. The ungrazed treatment had significantly more biomass than the grazed treatment in 1994 and 1995 shoot cohorts, but biomasses of the 1996 shoot cohort were similar. The biomass of shoots older than 1994 appeared to be greater in the grazed plants but the difference was not significant. Mean plant biomass at the end of the experiment was greater in Horseshoe Park than in Moraine Park (1,830 g and 830 g, respectively; $P = 0.05$); however, the interaction between parks and grazed treatments was not significant for any of the variables measured.

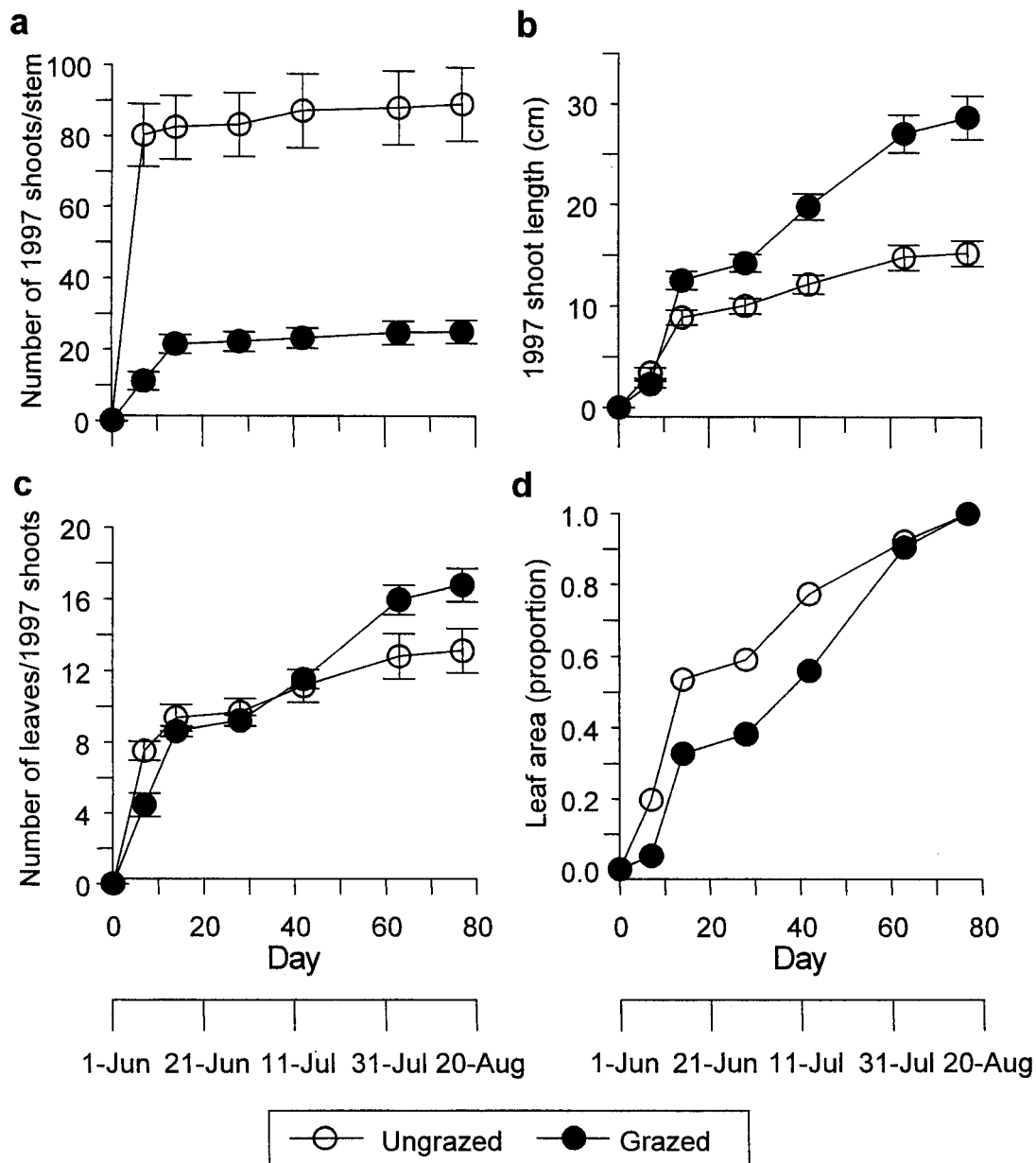


Fig. 2. Number of 1997 shoots per stem (a), 1997 shoot length (b), number of leaves per 1997 shoots (c), and proportion of total leaf area (d) through the growing season. Values indicate means of the ungrazed and grazed treatments, and vertical bars indicate standard errors.

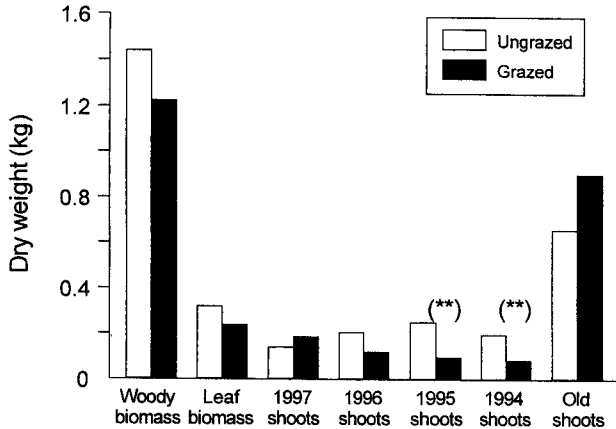


Fig. 3. Dry weight of total woody biomass and different plant components for the ungrazed and grazed treatments. References: (**) means are statistically different ($P < 0.01$).

No differences between treatments were found in the rate of change of leaves, or 1996 and 1997 shoot biomass when total plant biomass was used as a covariate. But, as expected, all slopes were significant ($P = 0.001$). Treatment means corrected for plant size were different only in the case of 1997 shoot biomass ($P = 0.05$). When the 1997 shoot biomass was analyzed using leaf biomass or leaf area as a covariate, grazed plants showed a higher slope ($P < 0.001$) and corrected mean ($P < 0.01$). These results indicated that grazed plants produced more shoot biomass per unit of leaf biomass or leaf area. In addition, grazed plants produced more 1997 biomass when corrected by the 1996 shoot biomass ($P = 0.009$). This latter result is probably related to the observed difference in the branching pattern of plants of different treatments. Almost all shoots formed by the ungrazed plants were developed from previous-year shoots (1996), but in the grazed treatment, many 1997 shoots were developed from shoots older than 1 year (epicormic shoots). The number of epicormic shoots was as high as 30% in grazed willows, while few shoots (less than 3%) of the willows inside the exclosures were epicormic (Peinetti 2000).

Gas Exchange

Gas exchange variables obtained at the beginning of the season did not differ between treatments. The rate of photosynthesis was not correlated with light intensity ($P = 0.2$), but transpiration was positively correlated ($P = 0.03$) in the restricted range of light intensities over which measurements were performed (1,000–

2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Water use efficiency (WUE) showed a linear decrease with higher light intensity in this range of radiation ($r = 0.81$; $P = 0.004$). In the second series of measurements, a wider range of microclimatic conditions was covered, but no treatment effects were found for any of the gas exchange variables. In this case, photosynthesis rates increased with increasing light intensity up to approximately 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ($r = 0.59$; $P = 0.0001$). Beyond this level, photosynthesis rates no longer correlated with light intensity ($P = 0.31$) (Fig. 4a). Photosynthesis rates tended to increase with increasing temperature, but the two variables are not well correlated ($r = 0.25$; $P = 0.03$) (Fig. 5a). Conversely, transpiration followed a linear increase with light intensity as in the first set of measurements, and an exponential increase with temperature (Figs. 4b and 5b). WUE tended to decrease with radiation but the

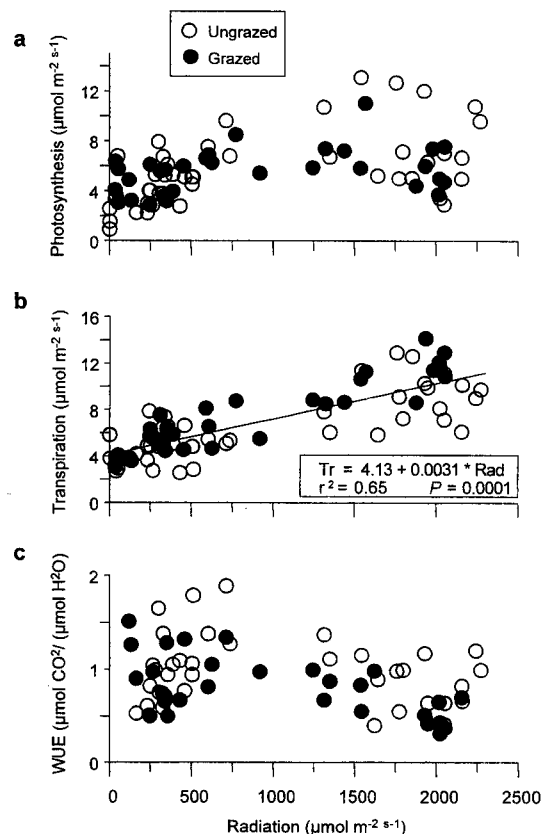


Fig. 4. Photosynthesis (a), transpiration (b), and water use efficiency (WUE) (c) as a function of light intensity in ungrazed and grazed treatments. WUE values at a light intensity lower than 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are not shown. The regression model was constructed with values of both treatments.

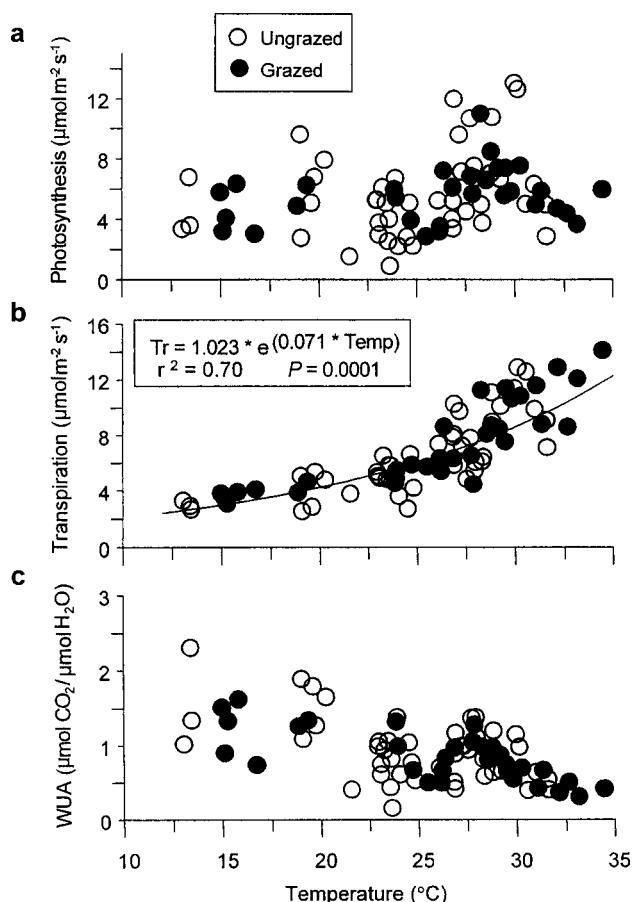


Fig. 5. Photosynthesis (a), transpiration (b), and water use efficiency (WUE) (c) as a function of temperature in the ungrazed and grazed treatments. The regression model was constructed with values of both treatments.

correlation between these two variables was low ($r = -0.29$; $P = 0.01$; Fig. 4c). WUE displayed a weak negative linear relationship with temperature ($r = -0.33$; $P = 0.0001$; Fig. 5c). At light intensities lower than $100 \mu\text{mol m}^{-2} \text{s}^{-1}$, high values of WUE were found due to very low levels of transpiration (data are not shown in Fig. 4c).

Light intensity was the variable showing the highest variability within the canopy of plants of both treatments ($P = 0.001$). Plant canopies reduced the light intensity that had reached the upper canopy by 10%, although light reductions to less than 50% of the upper canopy were not uncommon. Temperatures tended to be lower in the lower part of the canopy ($P = 0.001$), with differences as high as 2°C . CO_2 concentrations tended to be higher in the lower canopy ($P = 0.003$). Changes in environmental

correlation conditions affected gas exchange variables, with photosynthesis and transpiration consistently higher in the upper canopy ($P < 0.01$), but with similar WUE ($P = 0.09$).

Plant Nitrogen

The percent N in 1996 shoots seemed to be higher at the beginning of the season, and decreased thereafter until the end of the growing season when values increased again, probably due to translocation of N from leaves (Fig. 6). Leaves had highest N concentrations at the beginning of the season when they were not fully developed, with concentrations decreasing thereafter. A significant amount of N was retranslocated at the time of leaf senescence, producing a decrease in the N concentration of the leaves prior to litterfall. Grazed plants showed a higher leaf N concentration than ungrazed plants on some sample dates (Fig. 6). The percent N in 1997 shoots did not differ between treatments. At the beginning of the season, 1997 shoot N was higher than 1996 shoot N, but percent N decreased thereafter with increasing shoot length until the end of August. At this time, N concentration increased. It is interesting to note that this increase in N concentration did not correspond with the translocation of N from the leaves that occurred in the following month, but was coincident with the decrease in shoot extension growth (Fig. 2b).

Percent N in shoot cohorts did not differ between treatments. One-year shoots exhibited the highest percent N in woody biomass (1.16%; $P < 0.001$). In general, cohorts younger than 3 years showed higher percent N than older cohorts ($P < 0.01$; mean percent N in cohorts 4–12 years old was 0.42 ± 0.04). Leaves were the most important N sinks in the plant, but an important proportion of the total aboveground N was also allocated to the new shoots (Fig. 7a). The estimated total aboveground plant N content, and the N content of different plant compartments did not differ between treatments. However, on a relative basis, total plant N allocated into new shoots was significantly higher in grazed than ungrazed plants (0.11 vs. 0.19 1997 shoot N/total woody N; $P = 0.003$). Elk grazing reduced 1996 shoot N proportion to lower values than in ungrazed plants (0.08 vs. 0.047 1996 shoot N/total woody N; $P = 0.001$). The amount of N allocated to leaves relative to total plant N was similar between treatments ($P = 0.40$). However, on a relative basis, ungrazed plants retained more of the N invested in leaves than did grazed plants (Fig. 7b). The estimated N translocated from

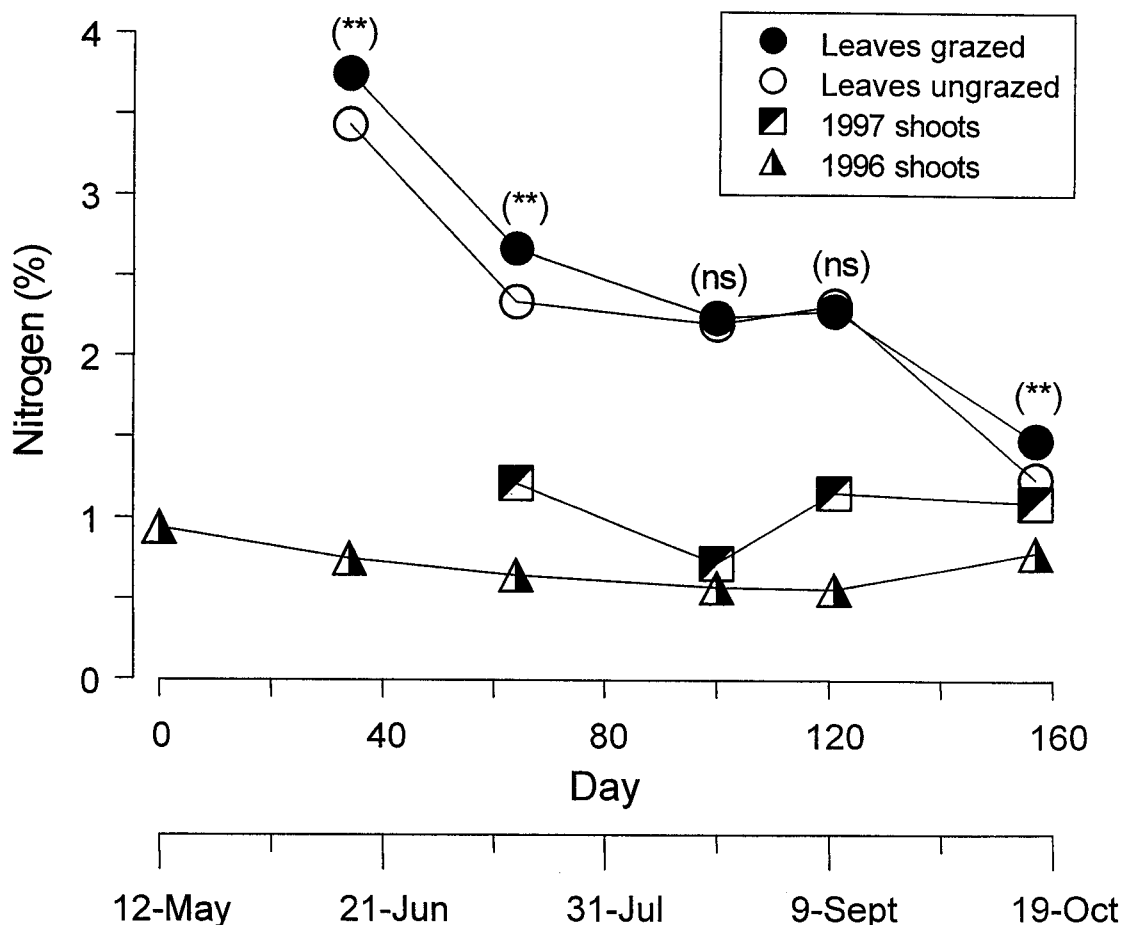


Fig. 6. Percentage of nitrogen in leaves, 1996 and 1997 shoots. Treatment means are represented only in the case of leaves. References: (**) means are significantly different ($P < 0.05$); (ns) means are not statistically different.

leaves was 3.9 g plant^{-1} in the ungrazed and 1.8 g plant^{-1} in the grazed treatment. These values were equivalent to the N allocated into the new shoot (1.6 and 2.1 g plant^{-1} for the ungrazed and grazed plants, respectively).

Discussion

Willows are grazed primarily during the winter and late summer, when most of the elk herd is on the winter range. Thus, the protection of grazed plants during the summer should not have produced any important changes in the natural pattern of willow utilization. Leaf stripping is the common form of elk grazing at the end of the summer, while during winter, elk select shoots

that developed in the previous growing season. Grazing on willow, as well as aspen (*Populus tremuloides*), has increased greatly on the winter range of RMNP in the last 30 years or so, due to an increase in the elk population (Hess 1993; Baker et al. 1997; Singer et al. 1998). Despite high winter grazing intensity, shoot and leaf productivities of short willow were not reduced. This type of response is considered compensatory growth (McNaughton 1979, 1983). Compensatory and overcompensatory aboveground growth were documented in graminoids under moderate herbivory (Briske and Richards 1995), and in woody species (Wolff 1978; Danell et al. 1985; Bergström and Danell 1987; Edenius et al. 1993; Hjältén 1999). However, total plant aboveground productivity provides a limited view of the

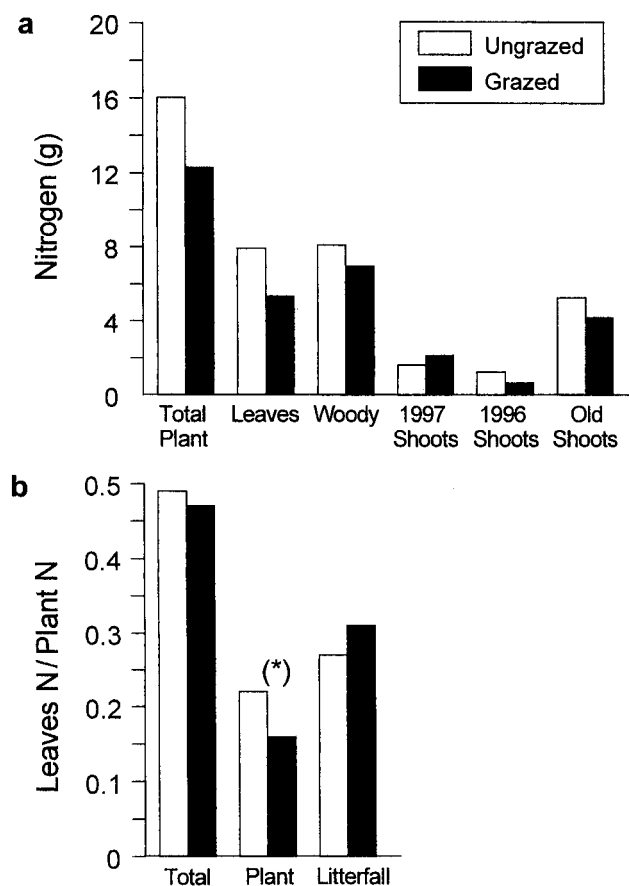


Fig. 7. Total nitrogen in the plant and in different plant components (a) and the ratio to total nitrogen of nitrogen recuperated by the plant and lost through litterfall (b). Bars represent mean values of ungrazed and grazed treatments (* means are statistically different at $P < 0.05$).

changes induced by grazing on woody plant performance. Other aspects need to be considered, in particular plant morphology (Jacobs 1969; Danell et al. 1985; Bergström and Danell 1987). Changes in plant morphology could, in turn, have different secondary effects. Elk grazing reduces the number of axillary meristems and constrains the number of buds available for new tissue development in the following growing season. Grazed willows seem to overcome this constraint by producing longer and thicker shoots, and increased branching by developing shoots from axillary meristems of shoots older than 1 year. Since leaves are produced only on new shoots, which were significantly reduced by grazing, the production of larger leaves was also a compensatory

response. All of these morphological changes have been documented as induced responses to winter grazing in other woody plants (du Toit et al. 1990), and in particular under winter grazing (Danell et al. 1994). Despite compensatory growth, continuous grazing will ultimately reduce plant height and size compared with ungrazed controls (Wolff 1978; Bergström and Danell 1987). After many years, plants protected from grazing differ from continuously grazed plants to the extent that they can no longer be used as controls for measuring grazing effects (Wambolt et al. 1998; see also Fig. 3). Similarly, in our experiment, after 3 years of protection, willows inside the enclosure were taller and had larger canopies than grazed willows. Plant height suppression occurred because elk preferentially grazed on shoots developed in the upper canopy. Height increase is considered an important strategy of woody plants to avoid grazing (Romme et al. 1995; Rohner and Ward 1997). Thus, by stimulating thicker and longer shoots and a lower shoot position, grazers generate a positive feedback between present and future grazing (Danell et al. 1985; du Toit et al. 1990; Romme et al. 1995). Increased palatability or reduction in concentration of secondary metabolites in grazed plants could also favor the development of this positive feedback (Danell et al. 1985; du Toit et al. 1990).

Other woody plant-grazer interactions involve a negative feedback mediated by plant secondary metabolites (Bryant et al. 1985). Elk grazing also induced the development of shoots from the lower part of the plant (old buds). These shoots do not contribute significantly to overall plant height increase but will make the canopy more compact. A more compact canopy will probably increase leaf overlap and reduce plant carbon input by self-shading. A strong gradient in microclimatic and gas exchange variables was found within the willow canopy. However, our data did not allow us to determine how different canopy architectures affect carbon input. Elk grazing also inhibited willow catkin production. Grazing reduced the number of axillary buds that are potentially available to develop into flowers during the next growing season. Flowering is probably inhibited because plants tend to prioritize vegetative growth as constrained by the number of axillary buds (Bergström and Danell 1987). Alternatively, continuously intense grazing induces a more juvenile pattern of development (Willard and McKell 1978; Bryant et al. 1985). A reduction in flower production is commonly documented in woody plants under grazing (Willard and McKell 1978; Katsma and

Rusch 1980; Bergström and Danell 1987). Intense grazing would have a significant negative effect on willow population ecology and fitness, if seed abundance were limiting (Paige and Whitham 1987).

Most studies of the effect of herbivory on plants that have demonstrated compensatory growth have been limited to measurements on aboveground biomass (Painter and Belsky 1993). However, increased aboveground productivity could result from a reduction in belowground carbon allocation instead of higher plant productivity. Our results seem to indicate that the compensatory response observed on grazed willows was the result of a reduction in the amount of carbon allocated belowground. We assume that the carbon gain by willows during the entire growing season is distributed between different plant compartments as follows:

$$NCI = LC + SC + WC + RC \quad (4)$$

where NCI = net carbon input, LC = leaf carbon, SC = new-shoot carbon, WC = carbon allocated in woody tissues older than 1 year, and RC = carbon allocated to roots. We found that grazed willows allocated more carbon in 1997 shoots than did plants of the ungrazed treatment:

$$SC_u < SC_b \quad (5)$$

where the subscripts u and b represent ungrazed and grazed plants, respectively. From equation 4, and considering that leaf biomass did not differ between treatments ($LC_u = LC_b$), then:

$$NCI_u - WC_u - RC_u < NCI_b - WC_b - RC_b \quad (6)$$

Assuming that the biomass derived from the growth of the cambium is a small proportion of total plant productivity and/or there was no difference between ungrazed and grazed plants in this biomass component, then:

$$NCI_u - RC_u < NCI_b - RC_b \quad (7)$$

Equation 7 indicates that grazed plants need to have a higher NCI in order to maintain a root carbon allocation similar to that of the ungrazed plants. The data showed no evidence of a higher NCI in grazed plants, as indicated by similar photosynthesis rates, total leaf areas, and leaf area dynamics in plants of both treatments. Together, these results indicate that there is a lower allocation belowground in grazed compared to ungrazed plants.

Woody plants probably tend to allocate more carbon aboveground in order to restore an allometric shoot/root ratio after grazing (Kramer and Kozlowski 1979). An increase in aboveground allocation is important for the plant to reestablish canopy photosynthesis capability (Briske and Richards 1995). Reduction of belowground biomass has been observed in grasses under herbivory (Coughenour 1985; Holland and Detling 1990), but no data are available for woody plants. If our inferences are correct, then persistent grazing will limit root growth, which will likely result in a shallower root system in grazed than in ungrazed plants. Since willows primarily use groundwater (Alstad et al. 1999), a shallow root system will reduce the ability of grazed willows to obtain water from a deeper water table. Consequently, reduction in the area influenced by the river and its associated water table, and changes in the river course that have occurred in this watershed have most likely increased willow mortality (Peinetti et al., this volume). Thus, this grazing intensity would probably reduce willow survival in those areas of the watershed where the water table has been deepened by shifts in stream channels.

Aboveground N concentrations in grazed plants are often higher than in ungrazed plants (Detling 1988; Briske and Richards 1995). Grazing also favors an increase in N concentration in woody plants (Danell et al. 1985; du Toit et al. 1990), but the response is variable, depending on the time that plants are grazed (Danell et al. 1994). Grazed willows showed higher percent N, but only in leaves. This pattern was not consistent throughout the entire growing season (see also Alstad et al. 1999). However, N concentrations in leaves and young shoots of willows varied due to growth and translocation, making the results difficult to interpret without considering the overall plant N balance. Grazed plants showed a more negative nitrogen balance than ungrazed plants because they recovered less N from leaves, and every winter they lost some nitrogen in the younger shoots to elk grazing. Nevertheless, percent N in the most active aboveground biomass (leaves and younger shoots) tended to be higher or similar to that of ungrazed plants. If the N pool is lower in the grazed willows at the start of the growing season, grazed plants will need to take up a higher proportion of N from the soil. In some deciduous species, a significant portion of the N that supports growth and reproduction comes largely from retranslocation out of senescing leaves (Chapin et al. 1990). A lower amount of stored N in grazed plants could be one reason for later growth initiation. Even though grazed plants compensate for lower N storage, late growth initiation could occur

because the time lags between microbial N mineralization in the soil, soil N uptake, and mobilization to the growing tips are probably longer than the time needed for N translocation from storage reserves. Grazed plants could mobilize more N from the soil if grazing increased soil N availability. Elk could increase N availability by various mechanisms, such as fecal and urine deposition (Frank et al. 1994; Hobbs 1996), by inducing lower carbon allocation to roots, which reduces microbial growth and N immobilization (Holland and Detling 1990), or by redistributing nutrients within the landscape (Afzal and Adams 1992; Russele 1992). Accordingly, elk herbivory in these willow communities has likely increased N return and litter quality, thus increasing long-term N cycling and availability (Menezes 1999).

Willow compensated for aboveground tissue removal by elk by increasing aboveground productivity. Despite this compensatory response, we infer that continuous grazing reduces plant performance by reducing root growth, particularly under the drier conditions generated by an increase in groundwater depth. Additionally, elk grazing induced important changes in plant morphology that constrained plant growth and development and modified carbon and N dynamics.

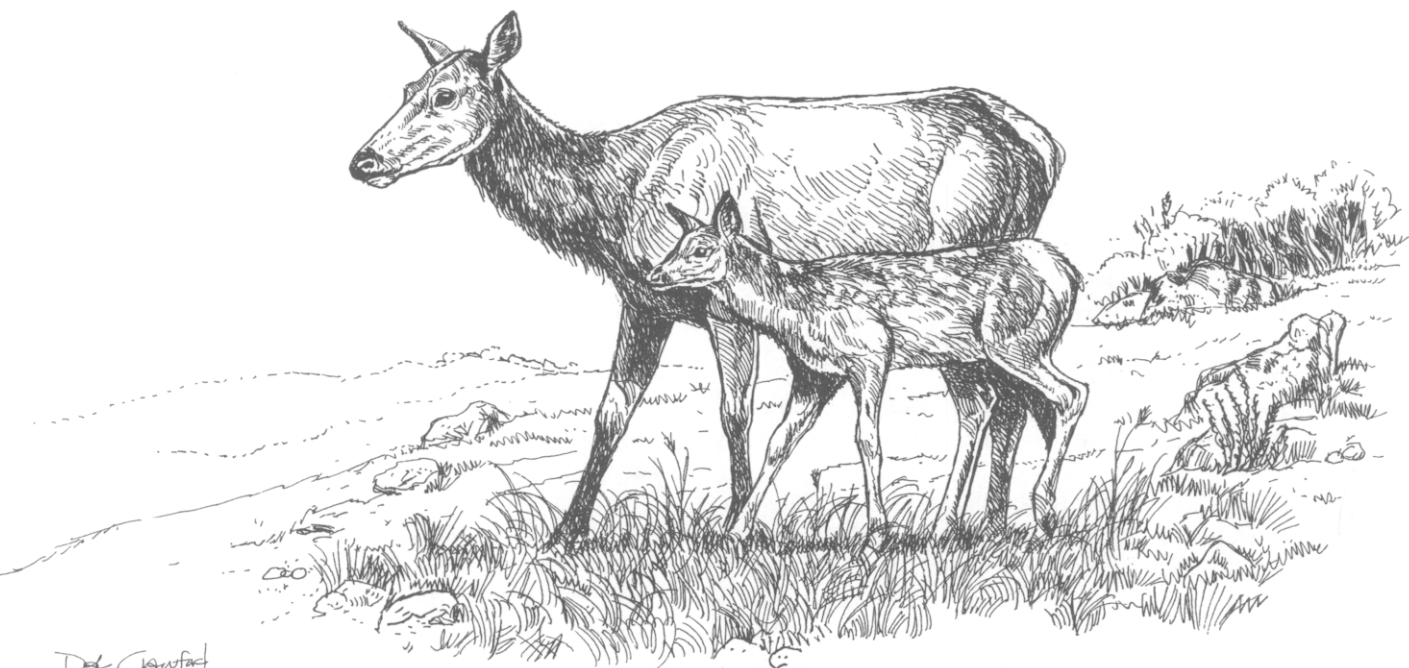
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